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Capture of Large Particles by Suspension-Feeding Scaleworm Larvae (Polychaeta: Polynoidae)

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Abstract. Most of the polychaete larvae in which feeding mechanisms have been studied feed using an opposed-band mechanism, capturing particles with prototrochal and metatrochal ciliary bands and transporting them to the mouth *via* a food groove. However, many other planktotrophic polychaete larvae lack a metatroch and food groove and thus must feed in a different way. In this latter group are the larvae of polynoid polychaetes, which not only lack a metatroch and food groove but also bear a bundle of long cilia (the oral brush) attached near the left side of the mouth. In feeding experiments with polystyrene beads and plankton, larvae of the polynoid *Arctonoe vittata* ingested larger particles (up to 60 μm in diameter) than those ingested by the opposed-band feeding larvae of the serpulid *Serpula vermicularis* (up to 12 μm in diameter). Videotaped images of feeding *A. vittata* larvae showed that capture behavior was elicited as particles in a feeding current driven by the prototroch approached or contacted the larval episphere. Particles on or very near the episphere were disengaged by a recoiling motion of the larva and were then moved to the mouth, probably by the oral brush. This feeding mechanism may be widespread in the polychaete superfamily Aphroditacea, which includes about 10% of extant polychaete species.

Introduction

The feeding mechanisms of polychaete trochophore larvae that have three equatorial ciliary bands (the prototroch, food groove, and metatroch) are relatively well understood (R.R. Strathmann, 1987). The long cilia of the prototroch beat from anterior to posterior, producing a current for both swimming and feeding. Some of the particles that pass within reach of the prototrochal cilia are swept into the food groove, possibly with assistance from the metatrochal cilia (which beat from posterior to anterior). Particles retained in the food groove are carried to the mouth. This "opposed-band" mode of particle capture has been documented in larvae of serpulid and oweniid polychaetes as well as in larvae of bivalve and gastropod molluscs (Strathmann *et al.*, 1972; Strathmann and Leise, 1979; Lacalli, 1984; Gallagher, 1988; Emlet and Strathmann, 1994). Work on the larvae of capitellid polychaetes and bivalve molluscs (Riisgård *et al.*, 1980; Fritz *et al.*, 1984; Sprung, 1984; Hansen, 1993) suggests that opposed-band feeders capture small particles (<10 μm) far more efficiently than large ones. This upper limit on the sizes of captured particles may be imposed by the dimensions of the feeding structures, in particular the length of the prototrochal cilia and the width of the food groove (R.R. Strathmann, 1987).

Many planktotrophic polychaete larvae, however, lack a metatroch and a food groove and thus must capture and handle particles differently than do opposed-band feeders. Such larvae (*e.g.*, glycerids, nephtyids, and phyllodocids) are often among the most abundant polychaete larvae in temperate waters (Lacalli, 1981; Yokouchi, 1991), but their feeding behavior is unknown. Larvae of polychaetes in the superfamily Aphroditacea (scaleworms) not only lack a metatroch and food groove, but also bear a single bundle of long cilia attached near the prototroch at the left side of the mouth and extending posteriorly (Fig. 1a, b, c). We will refer to this asymmetrically placed bundle of cilia as the oral brush, after Lacalli (1980). Whether the oral brush is involved in feeding is not known. Also unknown is how the feeding mechanism of scaleworm larvae might influence the size range of particles that they can capture and handle. The

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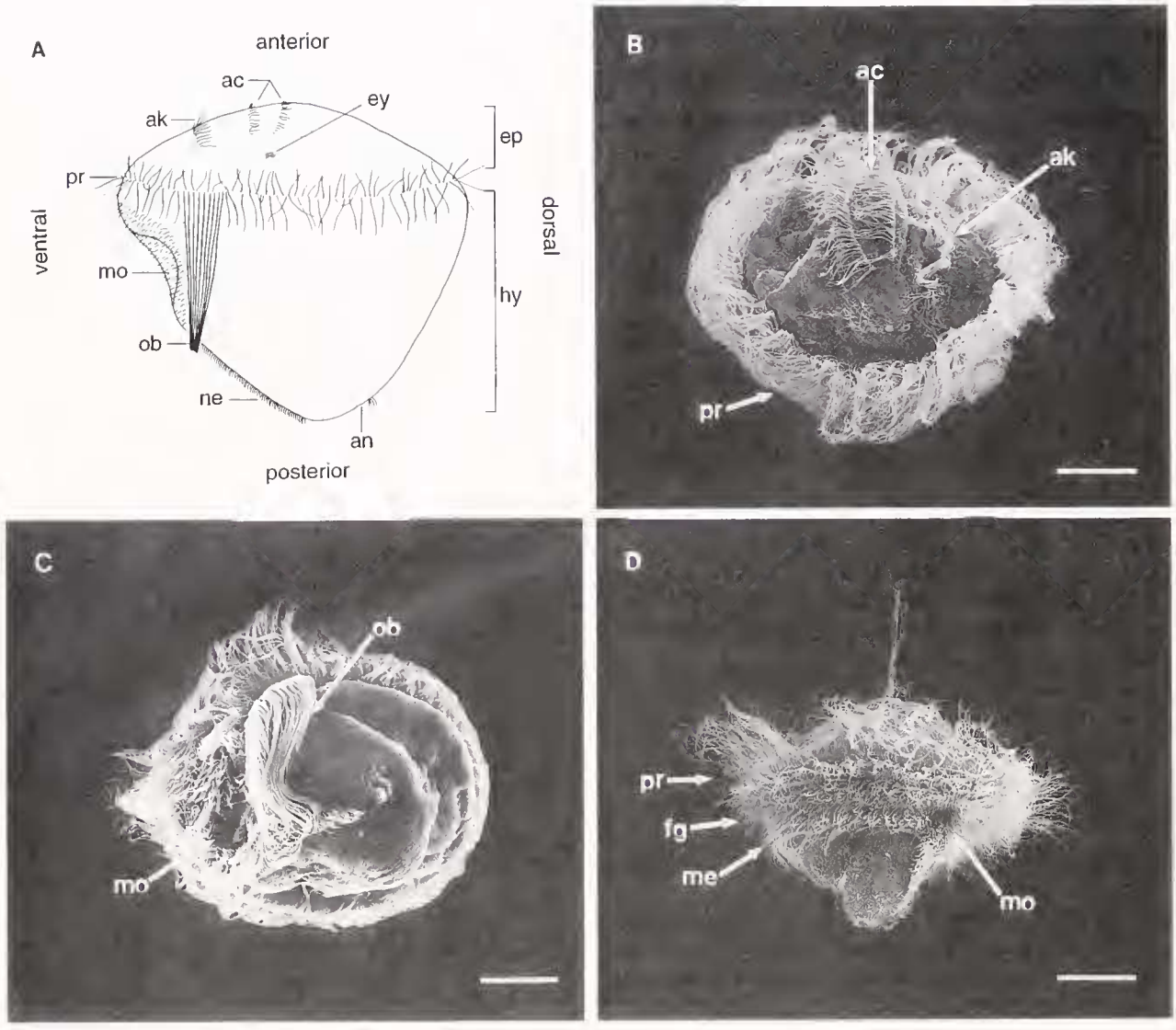

Figure 1. Larvae of *Arctonoe vittata* and *Serpula vermicularis*. (A) Line drawing of *A. vittata* larva, in left lateral view. (B) Scanning electron micrograph of 27-day-old *A. vittata* larva, in anterior view; the ventral side of the larva is to the right. Scalebar = 25 μm. (C) Scanning electron micrograph of 26-day-old *A. vittata* larva, in posterior view; the ventral side of the larva is to the left. Scalebar = 25 μm. (D) Scanning electron micrograph of 8-day-old *S. vermicularis* larva, in right lateral view. Scalebar = 25 μm. ac = apical cilia, ak = akrotroch, an = anus, ep = episphere, ey = eye, fg = food groove, hy = hyposphere, me = metatroch, mo = mouth, ne = neurotroch, ob = oral brush, pr = prototroch.

guts of scaleworm larvae captured from the plankton often contain particles much larger than 10 μm in diameter (*e.g.*, diatoms and bivalve veligers 30–100 μm in diameter: Lebour, 1922; Lacalli, 1981; Yokouchi, 1991).

In this paper we describe feeding in larvae of the polynoid scaleworm *Arctonoe vittata*. We compared the sizes of artificial and natural particles ingested in the laboratory by larvae of *A. vittata* and by similarly sized larvae of the serpulid *Serpula vermicularis*. Larvae of *S. vermicularis* have a prototroch, metatroch, and food groove, and they feed with the opposed-band mechanism described above (Strathmann *et al.*, 1972: Fig. 1d). In our experiments, *S. vermicularis* larvae fed only on particles 12 μm or less in diameter, a result consistent with the generalization that opposed-band feeders capture small particles more efficiently than large ones. *A. vittata* larvae, on the other hand, ingested particles up to 60 μm in diameter. Analysis of videotaped sequences of feeding *A. vittata* larvae showed that they used the prototroch to generate a feeding and locomotory current and the ciliated episphere to sense and capture particles. Captured particles were then transferred to the mouth, probably

by the oral brush. This previously undescribed feeding mechanism is probably widespread within the aphroditaceans, most of which have planktotrophic larvae with oral brushes.

Materials and Methods

Larval cultures

Adult specimens of *Arctonoe vittata* were collected with host keyhole limpets (*Diodora aspera*) in the intertidal zone on the west side of San Juan Island, Washington. Specimens of *Serpula vermicularis* were collected from Argyle Creek, San Juan Island. Spawning was induced in females of both species on 18 June 1995 by removing individuals from their hosts or tubes, respectively, and isolating them in small dishes of seawater. Oocytes spawned by one female of each species were briefly rinsed in 0.45 μm filtered seawater (FSW) and inseminated with sperm removed from the coelomic cavity of a single conspecific male. More than 90% of the eggs in each cross were fertilized. Larvae were cultured in 10 μm FSW at densities of approximately 200 larvae·l^{-1}. The cultures were stirred with a system of swinging paddles (M. Strathmann, 1987), and the culture jars were kept partially immersed in a seatable at 10°–13°C (near local ambient sea temperature). All larvae used in feeding experiments were starved for 12 h prior to the experiment; otherwise they were fed a mixture of *Rhodomonas* sp. (maximum dimension about 10 μm) and *Isochrysis galbana* (maximum dimension about 6 μm) every 3–5 days, immediately after water changes.

Sizes of ingested particles: polystyrene beads

This experiment was conducted to determine the size range of particles that larvae of each species would ingest. In preliminary experiments, larvae were fed suspensions of single size classes of beads (2, 10, 20, and 40 μm) and a single mixed suspension of these size classes Phillips (unpub. data). The size ranges of beads ingested by larvae in both of these experimental conditions were the same. Therefore, for the feeding experiment described here we used a single mixed suspension of multiple size classes of beads. We used spherical beads of diameters we shall refer to as 2, 10, 20, and 40 μm (the manufacturer's stated diameters were 2.12 μm [Duke Scientific, Bioclean, green-fluorescing], 9.87 ± 0.57 μm, 19.5 ± 0.6 μm, and 42.1 ± 0.8 μm [Duke Scientific, Size Standards, NBS Traceable]). We made stock suspensions of each bead size class in 0.45 μm FSW and made 6–10 replicate counts per size class in a hemacytometer (2-, 10-, 20-μm beads) or a Bogaroff tray (40-μm beads) to estimate concentrations. To eliminate clumps of beads, each suspension was placed in a bath sonicator for 5 min prior to counting. From these stocks we made a working mixed suspension consisting of 8340 2-μm beads·ml^{-1}, 4170 10-μm beads·ml^{-1}, 2085 20-μm beads·ml^{-1}, and 417 40-μm beads·ml^{-1}.

The bead-feeding experiment was conducted 8 days after fertilization. Larvae of *A. vittata* were distributed among five 20-ml glass vials (20 larvae/vial), and larvae of *S. vermicularis* were distributed similarly among another five vials. Aliquots (15 ml) of sonicated working suspension were introduced into each vial. To maintain particles in suspension, these vials were strapped to a revolving plankton wheel (0.025 revolutions·s^{-1}, diameter = 23 cm) and maintained at 12°C. Preliminary experiments suggested that larvae of the two species ingested particles at different rates (Phillips, unpub. data); therefore, *S. vermicularis* larvae were removed from the plankton wheel after 30 min, and *A. vittata* larvae were removed after 1 h. Larvae were killed immediately by the addition of formalin to a final concentration of approximately 5%.

The gut contents of as many larvae as could be recovered from each vial (15–19) were examined using an epifluorescence microscope. A fluorescein isothiocyanate filter (ex. = 420–490 nm, em. = 520 nm) was used to detect the 2-μm beads. All other beads were detected with normal brightfield optics. Beads were counted as ingested if they were found anywhere in the digestive system of the larva, and the number and sizes of beads ingested by each larva were recorded.

Sizes of ingested particles: concentrated natural plankton

To corroborate the results of the bead-feeding experiment, we conducted additional feeding experiments using natural plankton. We obtained concentrated natural plankton by towing a 25-μm-mesh net vertically off the breakwater at the Friday Harbor Laboratories. The concentrated plankton was passed through a 200-μm mesh to remove large particles and predators. Eight-day-old *A. vittata* larvae were placed into two 20-ml vials (20 larvae/vial), and 8-day-old *S. vermicularis* larvae were similarly divided between another two vials. Fifteen milliliters of concentrated plankton was added to each vial, and the vials were strapped to the plankton wheel used in the bead experiment, at 12°C. After 3 h larvae were examined alive (so that ingested particles could be better identified), immobilized in a suspension of polyethylene oxide in seawater, and the largest particles each had ingested were measured. Ten larvae of *A. vittata* from each of the two vials and 10 larvae of *S. vermicularis* from a single vial were examined. A second plankton-feeding experiment was conducted with 18-day-old larvae (15 of each species) under identical conditions.

Feeding by larvae of Arctonoe vittata: *videotaped observations*

Larvae of *A. vittata* maintained in unstirred cultures tend to become tethered to the bottom of the culture vessel by strands of mucus trailing from their posterior ends. We videotaped such tethered larvae in suspensions of particles to visualize particle capture and handling. About twenty 27- to 30-day-old *A. vittata* larvae from unstirred cultures were gently transferred to a small petri dish filled with 0.45-μm FSW. A suspension of 40-μm polystyrene beads was added, and the dish was covered with a glass microscope slide, excluding air pockets. Larvae in the dish were examined with a dissecting microscope equipped with a Sony HVM-200 video camera linked to a video recorder and monitor. Larvae that were tethered (little or no forward motion) but that continued to rotate normally were videotaped at a magnification of 40×. Larvae and seawater were changed every 30 min to minimize the effects of temperature increases. Although tethering undoubtedly influenced patterns of flow around larvae (*e.g.*, Emlet, 1990), it probably did not affect qualitative aspects of the mode of feeding that we describe.

Measurements of larvae

Eight-day-old and 18-day-old larvae were immobilized with a small amount of polyethylene oxide in seawater and examined alive with a compound microscope.

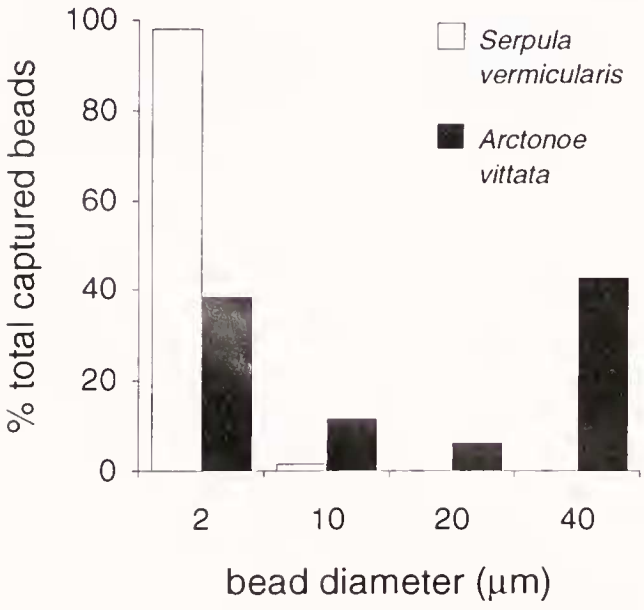

Figure 2. Percentage of beads in each size class captured by 8-day-old larvae of *Arctonoe vittata* and *Serpula vermicularis* in the bead-feeding experiment. Fifty-four *A. vittata* larvae ingested a total of 119 beads; fifty-two *S. vermicularis* larvae ingested a total of 116 beads.

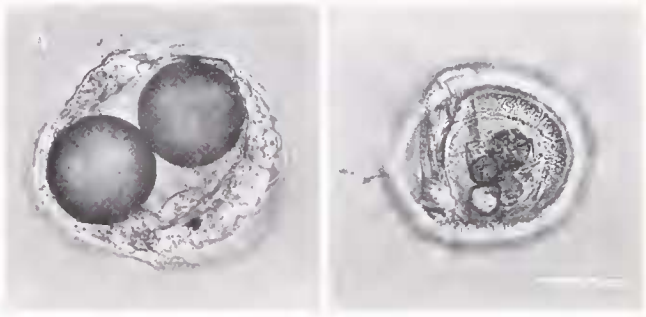

Figure 3. Light micrographs of *Arctonoe vittata* larvae that ingested particles in feeding experiments. Figures A and B are not to the same scale. (A) An 8-day-old larva (killed in formalin) with two polystyrene beads in its gut. Each bead is 40 μm in diameter. (B) An 18-day-old larva (live) in posterior view with several large particles from natural, concentrated plankton in its gut. Scalebar = 50 μm.

For larvae of both species we measured total body length, maximum body width (equivalent to prototroch diameter), prototrochal cilium length, and mouth width. In addition, we measured the width of the food groove in larvae of *S. vermicularis* and the length of the oral brush in larvae of *A. vittata*. Because it was difficult to manipulate larvae in polyethylene oxide, not all measurements were made on each individual. We used a one-way analysis of variance and *posthoc* tests (Scheffé's *F*-test: Sokal and Rohlf, 1981) to identify significant ($P < 0.05$) differences in size among the four groups of larvae measured.

Results

Sizes of ingested particles: polystyrene beads

Seventy-six larvae of *A. vittata* were recovered and examined. Of these, 54 (71%) had ingested 1–6 beads, and the remainder had not ingested any. Of 82 larvae of *S. vermicularis* 51 (62%) had ingested 1–12 beads, and the remainder had not ingested any. *A. vittata* larvae ingested beads over the whole size range offered, though most beads ingested were in the 2- and 40-μm size classes (Figs. 2, 3a). *S. vermicularis* larvae ingested mostly 2-μm beads, and they ingested no beads greater than 10 μm in diameter (Fig. 2).

Sizes of ingested particles: concentrated natural plankton

In the first plankton-feeding experiment, with 8-day-old larvae, all 20 *A. vittata* larvae and all 10 *S. vermicularis* larvae examined had ingested 1–10 particles ranging in maximum diameter from 3–12 μm; no larvae of either species had any larger particles in their guts.

In the second plankton-feeding experiment, with 18-day-old larvae, 15 larvae of each species were examined. Twelve of the 15 *A. vittata* larvae (80%) had ingested

from 1 to 5 particles 30–40 μm in diameter. These were mostly dinoflagellates (Fig. 3b). One *A. vittata* larva had ingested a 90-μm-long pennate diatom as well as a centric diatom 60 μm in diameter. Most of these larvae had also ingested many other unidentified particles smaller than 10 μm in diameter. Ten of the 15 *S. vermicularis* larvae (66%) had ingested visible particles; these were all smaller than 6 μm in maximum diameter.

Feeding by larvae of Arctonoe vittata: *videotaped observations*

We videotaped 10 particle captures by five different larvae. In five instances the larvae captured and ingested 40-μm beads; in three instances the larvae captured and rejected 40-μm beads; and in the remaining two instances larvae responded to small (<10 μm) particles present as contaminants. In these last two cases it was not possible to determine if the particles were successfully captured and ingested. The events of particle capture were similar in all instances observed.

The sequence of events in the capture and ingestion of a 40-μm bead is shown in Figures 4 and 5. The tethered larva rotated clockwise (viewed anteriorly) around its anterior-posterior axis at about 1 revolution $\cdot s^{-1}$, the prototroch creating a current in the anterior to posterior direction. A particle entrained in this current rapidly approached the larva (Figs. 4a, 5a), and came very near to or contacted the central portion of the episphere (Figs. 4b, 5b). The particle then moved ventrally on the episphere, towards the mouth of the larva (Figs. 4c, 5c). At this point the larva recoiled briefly, moving its entire body such that the particle was disengaged from the episphere (Figs. 4d, 5d). After the recoil, the larva continued its clockwise rotations. The bead, now located 80–90 μm (n = 3 captures) ventrally and slightly to the left of the mouth, rotated with the larva as if it was being held in that position (Figs. 4e–g, 5e–g). The larva and bead rotated together for 0.3–2 revolutions before the bead was seen at the mouth (Figs. 4h, 5h) and soon thereafter the bead was visible in the gut of the larva (Figs. 4i, 5i). The larva continued to rotate normally while the captured bead was held in front of the mouth and then ingested. We were unable to see the oral brush during particle capture or handling.

In all three instances in which a 40-μm bead was captured and then rejected, the events of capture were as described above. When rejection occurred it was always after the bead had been held in the mouth (as in Fig. 4h) for one or several revolutions. In two cases, the rejected bead slowly moved down the neurotroch before being released near the anus. In the other case the rejection path of the bead was not visible because of the orientation of the larva.

Measurements of larvae

Larvae of *A. vittata* increased in mean length, body width, prototrochal cilium length, and oral brush length between 8 and 18 days after fertilization (Table 1). Larvae of *S. vermicularis* decreased in body width over this time period. Mouth width did not change significantly in larvae of either species between 8 and 18 days after fertilization. Eight days after fertilization, larvae of *A. vittata* were smaller in length and diameter than larvae of *S. vermicularis;* these differences were no longer apparent 18 days after fertilization. Mouth width and prototrochal cilium length in *A. vittata* larvae were significantly greater than in *S. vermicularis* larvae at both 8 and 18 days after fertilization.

Discussion

The results of the bead- and plankton-feeding experiments demonstrate that the polynoid and serpulid larvae we observed ingest particles of different size ranges. The opposed-band feeding larvae of *Serpula vermicularis* ingested only small particles (≤12 μm) in all experiments, whereas larvae of *Arctonoe vittata* ingested particles 2–60 μm in diameter. Only in the first plankton-feeding experiment, with 8-day-old larvae, did larvae of the two species ingest particles of similar sizes (all ≤12 μm). That result may reflect the absence of larger particles in the plankton on that day. This interpretation is supported by the results of a bead experiment carried out simultaneously; here many 8-day-old *A. vittata* larvae ingested 40-μm polystyrene beads (Fig. 2). We did not determine the size distribution of particles in the plankton and cannot address this problem directly. For larvae of *S. vermicularis*, our results are consistent with the hypothesis that the dimensions of the prototrochal cilia or food groove set an upper limit on the sizes of particles that can be captured or handled (R.R. Strathmann, 1987). The mean sizes of both of these structures were larger than the maximum size of ingested particles in all feeding experiments.

Direct observations confirmed that the events of feeding by larvae of *A. vittata* are unlike those described for other trochophores. In tethered larvae of *A. vittata*, some of the particles carried in the feeding current approached very close to the surface of the episphere, and others appeared to directly strike the episphere (Figs. 4b, 5b). In all of the captures we observed, particles approached or contacted the central or ventral region of the episphere. Either the close approach or contact of particles with the episphere was sufficient to stimulate capturing behaviors. At this stage the particle may have simply been sensed by the larva, or it may have actually been captured on the surface of the episphere. The epispheres of many polynoid larvae, including those of *A. vittata*, bear

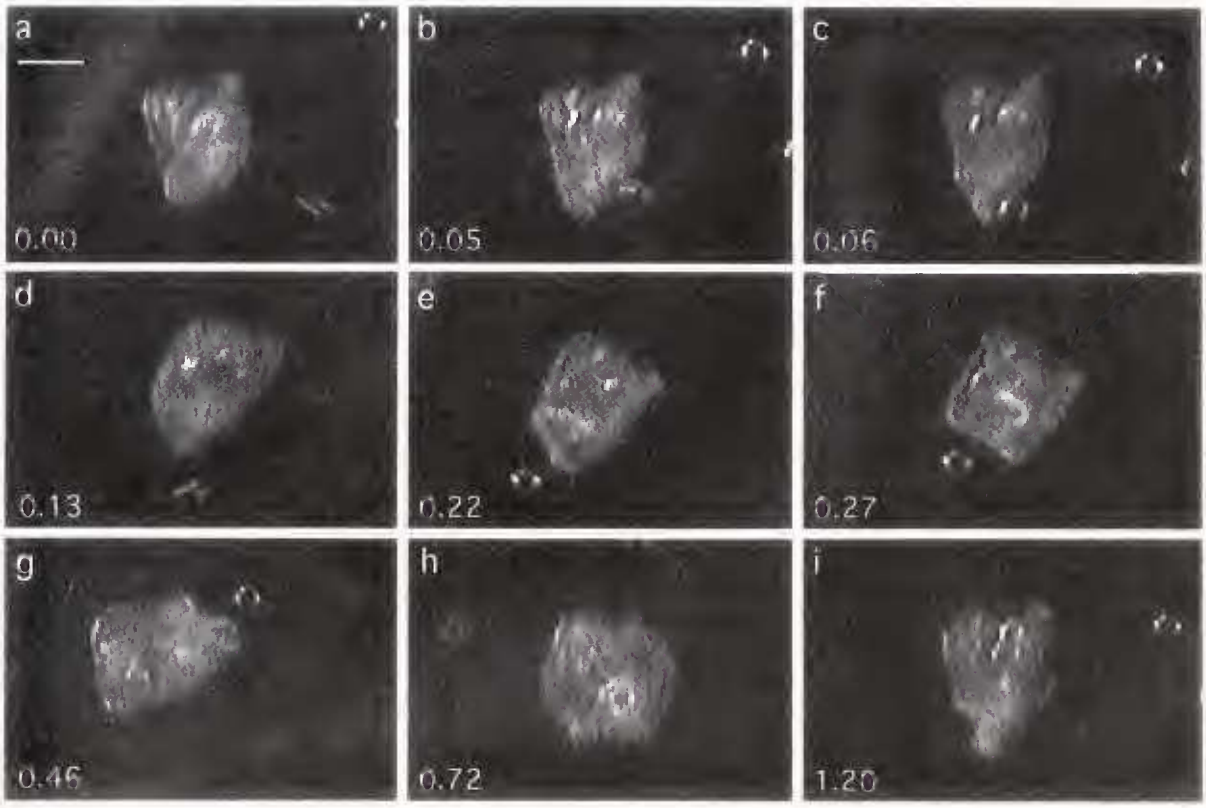

Figure 4. A sequence of videotape frames showing the capture of a 40-μm bead by a swimming, self-tethered *Arctonoe vittata* larva. Time (seconds) is in the bottom left corner. All images are at the same magnification; the scalebar is 100 μm. The larva is rotating around its anterior-posterior axis in a clockwise direction (when viewed from the anterior), and swimming towards the lower right of the image. (a) A bead approaches the larva's episphere. (b) The bead contacts the episphere. (c) The bead moves toward the upper lip. (d) The larva recoils and the bead is disengaged from the episphere. (e–g) The larva begins to rotate again, carrying the bead in front of and slightly to the left of the mouth. (h) After one full revolution the bead is held in the mouth. (i) The bead (as well as a previously captured bead) is visible in the gut.

several transverse ciliary bands (Fig. 1a, b: Cazaux, 1968; Holborow, 1969; Lacalli, 1981). In larvae of *A. vittata* (and larvae of *Harmothoe imbricata:* Holborow, 1969), the two bands located nearest to the episphere apex beat slowly and discontinuously; the band of cilia located between the episphere apex and the mouth (the "akrotroch," Fig. 1a, b) beats rapidly and continuously in the direction of the mouth (Pernet, pers. obs.). These ciliary bands may act in feeding by sensing approaching particles, distributing adhesive secretions over the episphere, or moving particles ventrally towards the mouth of the larva.

After the particle had been moved ventrally on the episphere, the tethered larva recoiled rapidly and then continued rotating. This recoiling motion, presumably a consequence of a brief reversal of beat of the prototrochal cilia, disengaged the particle from the region of the episphere, leaving it positioned about 80–90 μm ventral to and slightly to the left of the mouth (Figs. 4d–e, 5d–e). As the larva continued rotating, the particle remained in this position relative to the larval mouth, as if it was being held there (Figs. 4e–g, 5e–g). Based on these observations, we suggest that after the particle is disengaged from the episphere, the oral brush (normally carried parallel to the anterior-posterior axis of the body) is flung out ventrally where the particle is recaptured on its tip. Though lighting and limited magnification did not permit a clear view of the oral brush during captures, no other larval structure appears capable of effecting the observed movements of captured beads. The oral brush is attached on the left side of the mouth and is long enough to contact particles 80–90 μm distant (Table I: in the 27- to 30-day-old larvae used in these observations the oral brush was probably longer than 90 μm). How the particle might be held by the oral brush, or moved to the mouth, is not known. Perhaps the oral brush adheres to the particle, or perhaps the particle is held there by flow around it.

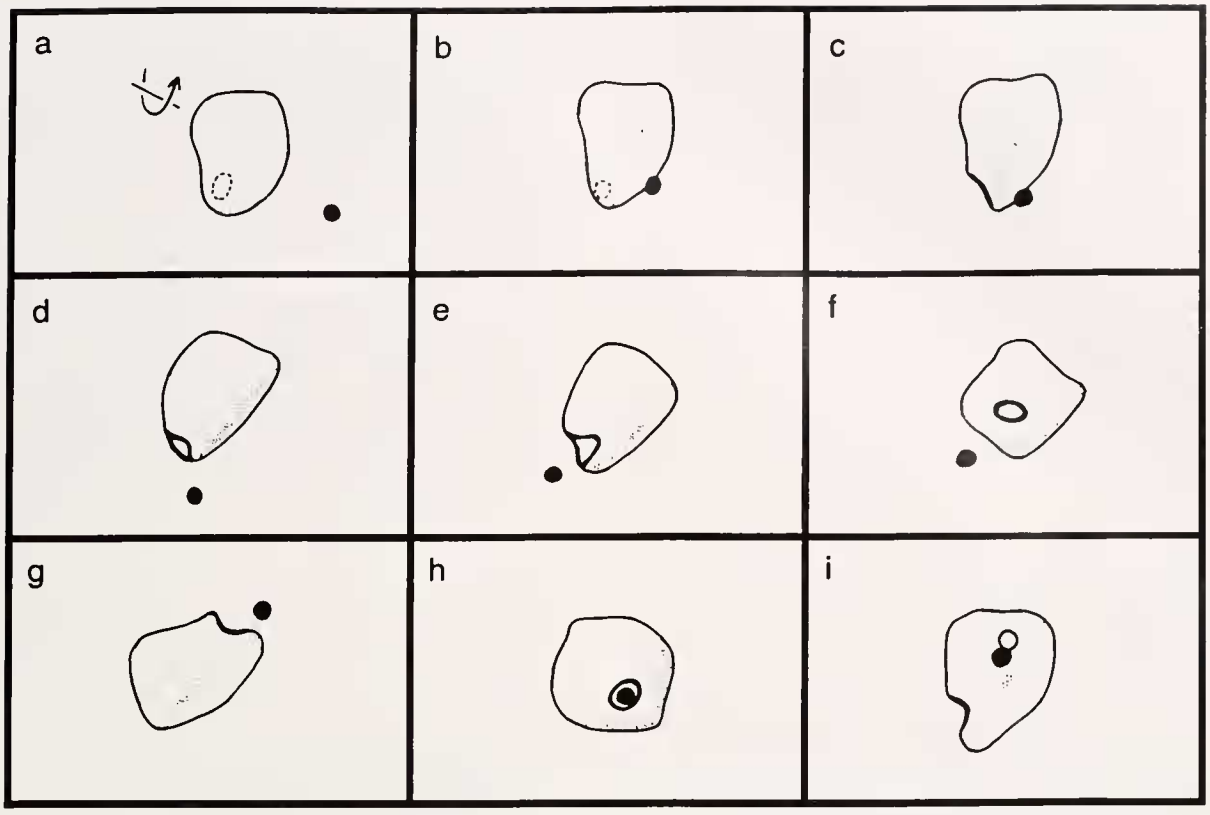

Figure 5. Line drawings of the video sequence shown in Figure 4; see the legend for that figure for details. The axis and direction of rotation of the larva is shown in (a). The stippled line represents the prototroch; the black sphere is the bead being captured; a previously ingested bead is represented as an open circle in (i). In (a) and (b) the mouth, on the opposite side of the larva from the observer, is represented by a dashed line. As the mouth comes into view (c–i) it is outlined with a heavy line. The oral brush is not shown.

The feeding mechanism we describe resulted in the capture of 40-μm particles. However, larvae of *A. vittata* also captured many smaller particles in feeding experiments (*e.g.*, Fig. 2). It is unlikely that these were ingested in the form of larger clumps of associated particles, because many larvae had ingested only one or a few small particles. Also, larvae in cultures captured and ingested the relatively small ($\leq$10 μm) algal cells that they were fed. Videotape observations showed that larvae responded to these particles with behaviors similar to those exhibited in response to 40-μm particles. However, because these small particles were difficult to see, we were

Table I

Sizes of Serpula vermicularis *and* Arctonoe vittata *larvae at 8 and 18 days post-fertilization*

	Serpula vermicularis		*Arctonoe vittata*	
	8 days old	18 days old	8 days old	18 days old
Body length	115.2 ± 9.3 (15)	123.7 ± 10.2 (7)	94.2 ± 6.1 (13)	129.1 ± 12.6 (8)
Body width	119.7 ± 7.9 (11)	93.6 ± 10.5 (7)	89.6 ± 11.8 (13)	112.4 ± 8.7 (7)
Mouth width	19.2 ± 2.9 (13)	16.2 ± 3.6 (5)	32.4 ± 4.5 (10)	33.6 ± 7.1 (3)
Prototrochal cilium length	41.0 ± 3.8 (15)	40.6 ± 3.4 (7)	39.5 ± 4 (11)	51.8 ± 2.2 (5)
Food groove width	25.3 ± 2.7 (10)	25.9 ± 3.9 (7)	—	—
Oral brush length	—	—	63.1 ± 3.5 (11)	91.7 ± 2.3 (6)

Mean sizes are reported in μm ± standard deviations; in parentheses are the number of individuals measured in each category.

unable to discern if they were actually captured and ingested. It is possible that small particles are captured by the same mechanism as large particles. Alternatively, small particles may be captured by the prototrochal cilia in the same way as in opposed-band feeders. In this scenario, only particles captured by prototrochal cilia overlying the densely ciliated oral region (Fig. 1a) might be ingested; the lack of a food groove means that particles captured elsewhere cannot be transported to the mouth. The observation that intermediate-sized beads (10 and 20 μm) were captured less frequently than 2- and 40-μm beads (Fig. 2) supports the hypothesis that *A. vittata* larvae feed using two different mechanisms.

Larvae of *A. vittata* increased in size between 8 and 18 days of age (Table I), and some of these size changes probably had consequences for particle encounter and capture rates. For example, mean body diameter increased from 89.6 to 112.4 μm. This change is reflected by an increase in the cross-sectional area of the episphere. Increases in episphere cross-sectional area imply increases in the volume of water that can be surveyed for particles. The length of the oral brush also increased dramatically between 8 and 18 days of age. A longer oral brush may allow larger particles to be captured, or it may enhance the efficiency of particle handling. Finally, the length of the prototrochal cilia increased between 8 and 18 days of age, from 39.5 to 51.8 μm. In opposed-band feeders, increases in the length of prototrochal cilia are associated with greater angular velocities of cilia, faster movement of water, or higher clearance rates of particles (Emlet and Strathmann, 1994). In larvae of *A. vittata* such increases may result in an increase in the volume of water that is passed by the episphere and surveyed for particles. Though we only measured larvae until 18 days of age, in laboratory cultures larvae of *A. vittata* survive for up to 7–9 weeks, reaching a body diameter of about 300 μm and an oral brush length of about 120 μm (Pernet, pers. obs.). Hence, body-size-associated changes in feeding capabilities may be quite dramatic over the course of development in larvae of *A. vittata*.

There are few obvious constraints on the maximum sizes of particles that can be captured and handled by *A. vittata* larvae. The flexural stiffness of the oral brush may limit the size or density of particles that can be held in front of the mouth. Although the dimensions of the mouth and gut ultimately constrain the sizes of particles that can be ingested, these structures are quite distensible. The mean width of the mouth in *A. vittata* larvae was approximately 33 μm, and larvae ingested polystyrene beads and dinoflagellates up to 40 μm in diameter, and a centric diatom 60 μm in diameter. Neither are there obvious constraints on the minimum sizes of particles that can be captured and handled. It is possible that very small particles may not stimulate episphere sensory structures and thus may not lead to capture responses (a similar hypothesis was suggested by R.R. Strathmann [1987] to account for the relatively low clearance rates of small particles by echinoderm larvae). The oral brush is composed of very closely spaced cilia (Fig. 1c), and it seems unlikely that even very small particles are able to pass through it.

Although larvae of *A. vittata* can capture and ingest particles of a wide range of sizes, feeding efficiency may vary with particle size. In our bead-feeding experiment, for example, larvae of *A. vittata* ingested 2- and 40-μm beads far more frequently than 10- and 20-μm beads (Fig. 2), despite the fact that they were more likely to encounter the latter sizes in the bead suspension we used. (In direct interception, the mode of particle capture presumably used by these larvae, encounter rate is a function of both particle size and particle concentration [Shimeta and Jumars, 1991]. In our experiment the concentrations of 10- and 20-μm beads were such that they should have been encountered 2.5 times as frequently as 2- and 40-μm beads.) Such patterns may represent constraints imposed by the mechanisms of particle capture and handling. This may help explain the observation of Lacalli (1981) that the abundance of polynoid larvae in Passamaquoddy Bay, New Brunswick, is correlated with the abundance of large diatoms. He suggested that polynoid larvae feed more efficiently on large particles, and that larvae developing earlier or later than the local spring diatom bloom are doomed to high mortality because of a lack of suitably large particles to eat. Other workers have not found a clear correlation between the availability of large particles and the abundance of polynoid larvae (Cazaux, 1973; Yokouchi, 1991). Such linkages between the physical mechanisms of particle capture and the availability of appropriately sized food particles merit further study, and may be useful in understanding some of the selective forces leading to seasonal reproductive strategies in polynoids.

Oral brushes appear to be limited in distribution to larvae of aphroditaceans. The superfamily Aphroditacea includes at least 890 described species (Pettibone, 1982). At least 600 of these species are members of the family Polynoidae, and all known polynoid larvae are planktotrophic and bear an oral brush (Table II). The only other aphroditacean larvae that have been described belong to the family Sigalionidae, and most of these also lack a metatroch and food groove and bear an oral brush (Table II). Early trochophores of the nephtyid *Nephtys hombergi* have also been reported to bear an oral brush (Wilson, 1936), but other descriptions of this and other nephtyid larvae do not mention the presence of this distinctive bundle of cilia (Rasmussen, 1973; Lacalli, 1980). Larvae that lack a metatroch and food groove and bear an oral brush probably feed as do larvae of *A. vittata;*

Table II

Larval nutritional mode and presence or absence of oral brush in aphroditacean larvae

Family (approximate # of species)	Species	Larval nutrition*	Oral brush	Reference
Aphroditidae (70)	—	—	—	—
Eulepethidae (25)	—	—	—	—
Polynoidae (600)	*Acholoe astericola*	pl	yes	Davenport, 1954
	Arctonoe fragilis	pl	yes	Pernet, unpub. data
	Arctonoe pulchra	pl	yes	Pernet, unpub. data
	Arctonoe vittata	pl	yes	this study
	Halosydna brevisetosa	pl	yes	Blake, 1975
	Halosydna gelatinosa	pl	yes	Bhaud and Cazaux, 1987
	Halosydna johnsoni	pl	yes	Rossi, 1976
	Harmothoe imbricata	pl	yes	Cazaux, 1968
	Harmothoe impar	pl	yes	Korn, 1958
	Harmothoe longisetis	pl	yes	Cazaux, 1968
	Harmothoe lunulata	pl	yes	Cazaux, 1968
	Harmothoe sarsi	pl	yes	Korn, 1958
	Lagisca extenuata	pl	yes	Cazaux, 1968
	Lepidonotus clava	pl	yes	Cazaux, 1968
	Lepidonotus squamatus	pl	yes	Cazaux, 1968
	Lepidonotus sublevis	pl	yes	Simon, 1965
Pholoidae (15)	—	—	—	—
Polyodontidae (45)	—	—	—	—
Sigalionidae (160)	*Pholoe balthica*	pl	—	Petersen, cited in Wilson, 1991
	Pholoe inornata	pl	—	Rasmussen, 1956
	Pholoe minuta	pl	no	Heffernan and Keegan, 1988,
	Pholoe minuta	pl	yes	Lacalli, 1980
	Pholoe swedmarki	lec	—	Laubier, 1975
	Pholoe synopthalmica	lec	yes	Cazaux, 1968
	Sthenelais boa	pl	yes	Cazaux, 1968
	"Genus A"	lec	—	Wolf, 1984

* "pl" = planktotrophy, "lec" = lecithotrophy, and "—" = no data. Family-level classification as in Fauchald (1977). No larvae of aphroditids, eulepethids, pholoidids, or polyodontids have been described.

thus the larvae of up to 10% of the 8000 extant polychaete species (Pettibone, 1982) may feed using the mechanism we have described for *A. vittata*.

Because polychaetes use a greater diversity of larval feeding mechanisms than any other major group of marine invertebrates (Strathmann, 1978), and because of the important role that the trochophore larva has played in many phylogenetic schemes (*e.g.*, Nielsen, 1987), the history of evolutionary changes in the feeding mechanisms of larval polychaetes is of particular interest. Developing an understanding of how these mechanisms (*e.g.*, opposed-band feeding and the mode of feeding we describe here for polynoids) are evolutionarily related will require additional data on mechanisms of particle capture in other polychaete larvae, as well as robust phylogenies of the group. A recent phylogenetic analysis of polychaete families places the Aphroditacea within a large group of families whose feeding larvae lack metatroch, food groove, and oral brush (*e.g.*, Glyceridae, Nephtyidae, Phyllodocidae; G. Rouse and K. Fauchald, pers. comm.). These larvae are often found with large particles in their guts (Lebour, 1922; Mileikovskii, 1959; Lacalli, 1981; Yokouchi, 1991), but how they feed is unknown. Descriptions of particle capture by trochophores that feed without opposed bands and without oral brushes are likely to be particularly useful in assessing patterns of evolutionary change in the feeding mechanisms of larval polychaetes.

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